

# Predation by *Orius insidiosus* (Heteroptera: Anthocoridae) on Life Stages and Species of *Frankliniella* Flower Thrips (Thysanoptera: Thripidae) in Pepper Flowers

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Environ. Entomol. 33(3): 662–670 (2004)

**ABSTRACT** We compared predation of *Orius insidiosus* (Say) on adult and second instars of *Frankliniella occidentalis* (Pergande) and on adults of *F. occidentalis* and *F. tritici* (Fitch) in arenas with pepper flowers. Also, we compared the dispersal of these thrips in the presence and absence of the predator. For each experiment, two densities of thrips (10 and 20 total thrips) and two time exposures (10 and 34 h) were tested. Second instars were more likely to move from the flower where they were released than were *F. occidentalis* adults. *F. tritici* dispersed more than *F. occidentalis*. The presence of the predator enhanced movement by thrips from flowers in which they were released. Despite differences in prey movement, *O. insidiosus* successfully preyed on all types of prey that were offered. However, *O. insidiosus* appeared to deal differently with each type of prey. Predation of both larvae and adults was most likely to occur inside flowers. In trials with adults and second instars of *F. occidentalis*, larvae were significantly more vulnerable to predation than were adults. *F. tritici*, the more active species, may have been vulnerable to predation because of higher rates of encounter with the predator; however, *O. insidiosus* may have had greater attack success against the less active *F. occidentalis*. The ability of *O. insidiosus* to prey successfully on different life stages and species of thrips in complex environments indicates that it is an efficient predator of thrips and an important biological control agent.

**KEY WORDS** biological control, predator-prey interactions, generalist predators, prey vulnerability

GENERALIST ARTHROPOD PREDATORS ARE able to feed on a variety of prey, but are likely to show preferences for certain types of prey. Although these preferences can have profound implications for biological control, much remains to be known about how generalist predators select their prey (Coll and Ruberson 1998). Some generalist predators have a genetically heritable preference toward particular prey, but are able to switch to alternative prey when their preferred prey are scarce (Saint-Cyr and Cloutier 1996). Some generalist predators feed preferentially on particular prey because those prey occur in the predator's preferred habitat, and hence are more likely to be encountered by the predator (Cloutier and Johnson 1993). Other generalist predators select prey not because of nutritional superiority, but because of the vulnerability of the prey to predation (Lang and Gsödl 2001). This factor may be critically important when predators

encounter prey that are morphologically similar but differ in behavior.

Generalist predators of the genus *Orius* (Heteroptera: Anthocoridae) feed on a variety of prey, but they have a preference for flower thrips (Thysanoptera: Thripidae). Based on field observations of predation, Salas-Aguilar and Ehler (1977) suggested that thrips are the preferred prey of *Orius tricolor* (White). This observed preference may be driven more by the predator and prey having overlapping habitats than an inherent prey preference (Cloutier and Johnson 1993, Hansen et al. 2003). Even so, species of *Orius* are effective predators of thrips in field and greenhouse crops, where they are important biological control agents (van den Meiracker and Ramakers 1991, Sabelis and Van Rijn 1997, Funderburk et al. 2000, Ramachandran et al. 2001). Yet little is known of how species of *Orius* respond when encountering different life stages or species of thrips in flowers. In no-choice tests, species such as *O. insidiosus* (Say) and *O. minutus* (L.) typically consume more thrips larvae than adults (Isenhour and Yeargan 1981, Lichtenauer and Sell 1993). Also, in no-choice tests, Fritsche and Tamo (2000) found that *O. albipennis* (Reuter) consume more larvae of *Ceratothripoides cameroni* (Priesner) than of *Megalurothrips sjostedti* (Trybom), but they

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did not observe a corresponding preference between these species in choice tests.

A complex of thrips species in the genus *Frankliniella*, including *F. occidentalis*, *F. tritici* (Fitch), and *F. bispinosa* (Morgan), occurs in north Florida (Chellemi et al. 1994, Toapanta et al. 1996, Funderburk et al. 2000, Ramachandran et al. 2001), and their management is a key concern for vegetable producers. *O. insidiosus* is a key natural enemy of these species (Funderburk et al. 2000), but how this predator interacts with different life stages or species of these thrips is poorly known. Understanding the efficiency of *O. insidiosus* as a predator of these thrips and the behavioral interactions that occur between predator and prey can provide important insights on thrips dynamics at larger ecological scales and a better understanding of how to manage pest thrips. Ramachandran et al. (2001) showed that local movement of *F. occidentalis* among pepper flowers (*Capsicum annuum* L.) is limited, whereas *F. tritici* move rapidly between pepper flowers. This assertion regarding differential movement was corroborated by Hansen et al. (2003), who showed that *F. occidentalis* is less active than *F. tritici*. Although *O. insidiosus* may not have any preference among life stages or species of thrips, the mobility of thrips may affect their vulnerability to predation. Therefore, *F. occidentalis* could be more vulnerable to predation than *F. tritici*, and larvae could be more vulnerable than adults because larvae move less and more slowly than adults (Sabelis and Van Rijn 1997).

We conducted four experiments to test these hypotheses. The first experiment was to determine the dispersal from pepper flowers of the adults and larvae of *F. occidentalis* in the absence of *O. insidiosus*. A second experiment was conducted to determine whether *O. insidiosus* has a preference for adults or larvae of *F. occidentalis*, and to determine whether the dispersal from pepper flowers of the adults and larvae changes in the presence of the predator. The third experiment was to determine the dispersal among pepper flowers of the adult *F. occidentalis* and *F. tritici* in the absence of *O. insidiosus*. A fourth experiment was conducted to determine whether the dispersal of *F. occidentalis* and *F. tritici* among pepper flowers changes in the presence of *O. insidiosus*, as well as to determine whether *O. insidiosus* preys differentially on these two common species.

### Materials and Methods

**Insect Colonies.** *O. insidiosus* were reared in 12.5 × 12.5 × 4.5-cm plastic containers maintained in a growth chamber at 28 ± 1°C, 60% RH, and a photoperiod of 14:10 h (L:D). Container lids had a 3 × 3-cm opening covered with thrips screen (Bioquip, Rancho Dominguez, CA). *O. insidiosus* were provided *F. occidentalis* and eggs of *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) as prey, and green bean pods (*Phaseolus vulgaris* L.) as an oviposition substrate. Water was provided, using a vial plugged with a cotton dental wick.

Thrips were reared in containers similar to those used for *O. insidiosus*. Green bean pods were provided as a food source and oviposition substrate. A thin streak of honey was placed on bean pods to provide additional nutrients. A 30-ml cup filled with damp vermiculite was added to provide extra moisture in the containers of *F. tritici*. Containers of the thrips were kept in growth chambers maintained at 28 ± 1°C, 60% RH, and a photoperiod of 14:10 h (L:D). Cohorts were staged to provide similarly aged insects for use in experiments. Voucher specimens of all species are deposited in the collections of the authors.

Newly opened (<12 h) pepper flowers were obtained from greenhouse-grown plants ('Yolo Wonder') that were grown in 3.79-liter pots with a commercial potting soil mixture. Each plant was treated with 330 ml of a high phosphorous fertilizer (9-59-8 N-P-K, 1.14 g/liter; Ferti-Lome, Voluntary Purchasing, Bonham, TX) twice per week to enhance blooming.

**Experimental Protocols.** Four experiments were conducted. For each experiment, two densities of thrips (10 and 20 total thrips) and two time exposures (10 and 34 h) were tested, for a total of four treatments per experiment. Each treatment in each experiment was replicated 10 times. Experimental arenas were maintained in growth chambers at 28°C, 60% RH, and at 14:10 h (L:D).

In experiment 1, the dispersal from pepper flowers of the adults and larvae of *F. occidentalis* in the absence of *O. insidiosus* was determined. Arenas for these trials were petri dishes (150 × 25 mm). Each petri dish contained one water-filled vial for a pepper flower, located in the center of the arena. The arena cover had a cap above the central flower, where thrips were released on the flower. Arena covers had three openings covered with thrips screen to provide ventilation and to prevent condensation. Arenas were sealed with parafilm to prevent insects from escaping.

At the beginning of each replicate, equal numbers of second instar and adult female *F. occidentalis* were collected from the colony with an aspirator and released through the cap onto the pepper flower. At the conclusion of each replicate, the flower was collected in a vial of 70% ethanol; thrips not in the flower were collected in a separate vial of ethanol. Numbers of adults and larvae in each location (i.e., in flower or outside of flower) were determined by examination of thrips with a stereomicroscope (×63).

In experiment 2, the dispersal from pepper flowers of the adults and larvae of *F. occidentalis* in the presence of the predator and the preference of *O. insidiosus* for adults and larvae of *F. occidentalis* were determined. Arenas were configured as in experiment 1. Thrips and *O. insidiosus* were handled using the same procedures as in experiment 1. Adults and second instars of *F. occidentalis* were released onto the flower. *O. insidiosus* were kept without prey for 20–24 h before being introduced into an arena. One hour later, the *O. insidiosus* was released into the arena. Only adult female *O. insidiosus* were used. Flowers and thrips were collected, as described for experiment 1.

Table 1. Maximum likelihood ANOVA for model parameters of prey type, and location for different densities and time exposures of adult and second instar *F. occidentalis* in the absence of *O. insidiosus*

Effect <sup>a</sup>	df	10 Insects/10 h		10 Insects/34 h		20 Insects/10 h		20 Insects/34 h	
		$\chi^2$	P	$\chi^2$	P	$\chi^2$	P	$\chi^2$	P
Location	1	21.07	<0.0001	2.11	0.1467	37.33	<0.0001	3.45	0.0631
Life stage	1	4.77	0.0290	1.19	0.2755	11.91	0.0006	1.54	0.2145
Location $\times$ life stage	1	7.87	0.0050	38.49	<0.0001	26.46	<0.0001	69.39	<0.0001

<sup>a</sup> Location = in or out of the flower. Life stage = adult or larvae of *F. occidentalis*.

At the conclusion of each replicate, the location of thrips and their status (i.e., consumed by *O. insidiosus* or not) were determined using a stereomicroscope ( $\times 63$ ).

In experiment 3, the dispersal among pepper flowers of the adult *F. occidentalis* and *F. tritici* in the absence of *O. insidiosus* was determined. The arena configuration was similar to that described for experiment 1, except that each petri dish contained four small water-filled vials for pepper flowers, located on the floor of the arena. One vial was located in the center of the arena. The other three vials were each placed 45 mm from the central flower vial, with a 120° arc between adjacent vials.

Thrips were handled and released using the same procedures as in experiment 1. At the beginning of each replicate, *F. occidentalis* and *F. tritici* were released through the cap onto the central pepper flower. At the end of each replicate, each flower was collected in a vial of 70% ethanol; thrips not in the flowers were collected in a separate vial of ethanol. Numbers of *F. occidentalis* and *F. tritici* in each location (i.e., in each flower or outside of flowers) were determined, as described for experiment 1.

In experiment 4, the dispersal of the adult *F. occidentalis* and *F. tritici* among pepper flowers in the presence of *O. insidiosus* and the preference of the predator for adults of these two thrips species were determined. Arena configuration, collection of flowers, and release of *F. occidentalis* and *F. tritici* were the same as described for experiment 3. One hour after the release of thrips, a female *O. insidiosus* was released into the arena through an opening offset from any flower. *O. insidiosus* were kept without prey for 20–24 h before being introduced into an arena. At the conclusion of each replicate, the location of thrips and their status (i.e., consumed by *O. insidiosus* or not) were determined.

**Data Analysis.** Log-linear models were fitted to the data for each experiment to analyze associations among the variables (Schoenig and Wilson 1992, Sokal and Rohlf 1995). These analyses allow testing for differences in the distribution of thrips and predation. For each experiment, a hierarchy of models was tested, starting with the fully saturated model, which included all possible terms. Initial terms included in the models were time, density, status (dead or alive for experiments 2 and 4), location (in or out of the flower of release), thrips type, and all possible interactions. Because of strong time and density interactions, treatments for each experiment were analyzed separately.

Therefore, saturated models for experiments 1 and 3 included the terms: status, location, thrips type, status  $\times$  location, status  $\times$  thrips type, location  $\times$  thrips type, and status  $\times$  location  $\times$  thrips type. For experiments 2 and 4, saturated models included the terms: location, thrips type, and location  $\times$  thrips type.

For each time and density combination of an experiment, a saturated model with all possible interactions was fitted to the data first, and then the significance of each term, starting with the highest order interaction, was analyzed by dropping that term from the model and determining the fit of the reduced model. If higher order interactions were not significant, lower order interactions were tested for significance. Nonsignificant interactions indicate that there is no association between the particular variables. This process of fitting models continued until no more terms could be dropped from a model. The resulting model would be the final model. Because the number of thrips in each treatment was fixed, this term was included in all final models. If particular interactions are not significant (i.e., not retained in final models), it indicates that those variables are independent (Sokal and Rohlf 1995). To test the distribution of adults, contrasts were made between the proportions in flowers versus outside of flowers, and between the proportions in the central release flower and the other flowers. All log-linear models for each experiment were computed using PROC CATMOD (SAS Institute 1989). In cases in which significant three-way interactions were present, specific two-way tests of independence were made. Where appropriate, means with 95% confidence intervals are given.

## Results

**Dispersal of Adult and Second Instar *F. occidentalis* in the Absence of *O. insidiosus*.** The significant location  $\times$  life stage interactions indicate that the larvae were more likely than the adults to disperse from the flower (Table 1; Fig. 1). After 10 h, >95% of adults were in the flower, whereas 28–43% of larvae were located outside of the flower. The proportion of larvae exiting the flower increased with time. At 34 h post-release, over 80% of the larvae had moved out of the flower, but <22% of the adults were outside of the flower.

**Dispersal of Adult and Second Instar *F. occidentalis* in the Presence of *O. insidiosus*.** There was a three-way location  $\times$  life stage  $\times$  predation interaction in the treatments in which *F. occidentalis* adults and lar-

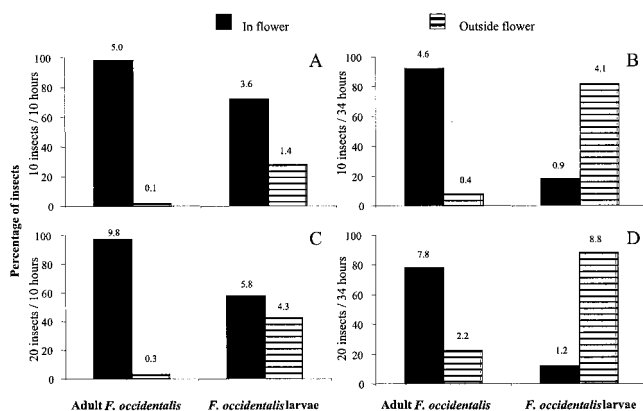


Fig. 1. Distribution of second instar and adult female *F. occidentalis*, at different densities and times after release onto a pepper flower, in the absence of *O. insidiosus*. The different densities and time intervals are (A) 10 insects at 10-h postrelease, (B) 10 insects at 34-h postrelease, (C) 20 insects at 10-h postrelease, and (D) 20 insects at 34-h postrelease. Numbers above bars are means.

vae were exposed to *O. insidiosus* (Table 2; Fig. 2). This interaction indicates that the association between predation and location (inside or outside of the flower) depended upon life stage (adult or immature). Significantly more larvae than adults were outside of the flower, yet almost all of the predation (87–100% of all predation) occurred within the flower. The proportion of the larvae that dispersed from the flower was similar in the 10-h exposures in the presence and absence of *O. insidiosus*. However, the proportion of the larvae dispersing from the flower was reduced by >50% in the 34-h exposure trials with *O. insidiosus* compared with the 34-h trials without *O. insidiosus*, most likely because predation on larvae had occurred already in the flower (Figs. 1 and 2). For all four time and density combinations, predation was significantly greater on larvae than on adults ( $P < 0.05$ ,  $G$  tests for independence; Fig. 2). At the low density of 10 thrips per arena, the total number of larvae and adults that were preyed upon increased substantially with time (10-h exposure,  $2.6 \pm 1.06$ ; 34-h exposure,  $5.3 \pm 1.89$ ). In contrast, at the higher density of thrips, the numbers of adults and larvae preyed upon remained nearly constant with time (10-h exposure,  $5.1 \pm 1.96$ ; 34-h exposure,  $5.3 \pm 1.89$ ). Because the absolute numbers of adults and larvae preyed upon in the two 34-h

exposure treatments were similar, but not in the two 10-h exposures, prey availability for *O. insidiosus* may have been limited at the lower density.

**Dispersal of *F. occidentalis* and *F. tritici* in the Absence of *O. insidiosus*.** In the two low-density treatments, there were no significant species  $\times$  location interactions, indicating that the distributions of *F. occidentalis* and *F. tritici* among the pepper flowers did not differ significantly (Table 3; Fig. 3). There was a significant location effect in both of the low-density treatments (Table 3). This effect resulted from the thrips being more likely to be in flowers than outside of the flowers (contrast between inside flowers and outside of flowers:  $\chi^2 = 17.41$ ,  $df = 1$ ,  $P < 0.0001$  for 10-h exposure;  $\chi^2 = 6.47$ ,  $df = 1$ ,  $P = 0.01$  for 34-h exposure). Thrips were more likely to disperse out of the central release flower over time. There was a significantly higher proportion of adult thrips in the central release flower than in the other flowers in the 10-h exposure (contrast between central release flower and outer flowers:  $\chi^2 = 15.00$ ,  $df = 1$ ,  $P < 0.0001$ ), but such a difference was not apparent in the 34-h exposure trial ( $\chi^2 = 1.02$ ,  $df = 1$ ,  $P = 0.31$ ). In the 10-h low-density exposure, the mean number of *F. occidentalis* per flower was  $3.8 \pm 0.88$  in the central flower compared with  $0.3 \pm 0.29$  (per flower) in the

Table 2. Maximum likelihood ANOVA for model parameters of predation, location, and life stage type for different densities and time exposures of adult and second instar *F. occidentalis* to *O. insidiosus*

Effect <sup>a</sup>	df	10 Insects/10 h		10 Insects/34 h		20 Insects/10 h		20 Insects/34 h	
		$\chi^2$	P	$\chi^2$	P	$\chi^2$	P	$\chi^2$	P
Status	1	18.81	<0.0001	5.66	0.0173	33.49	<0.0001	40.79	<0.0001
Location	1	16.35	<0.0001	17.72	<0.0001	35.47	<0.0001	12.62	0.0004
Life stage	1	1.15	0.2826	2.05	0.1522	1.97	0.1602	0.05	0.8298
Predation $\times$ location	1	6.43	0.0112	19.95	<0.0001	11.24	0.0008	2.62	0.1058
Status $\times$ life stage	1	1.56	0.2122	3.44	0.0635	0.50	0.4775	12.91	0.0003
Location $\times$ life stage	1	1.93	0.1651	6.69	0.0097	0.88	0.3495	0.02	0.8901
Predation $\times$ location $\times$ life stage	1	5.83	0.0150	8.47	0.0036	9.34	0.0022	7.69	0.0056

<sup>a</sup> Predation = alive or dead. Location = in or out of the flower. Life stage = adult or larvae of *F. occidentalis*.

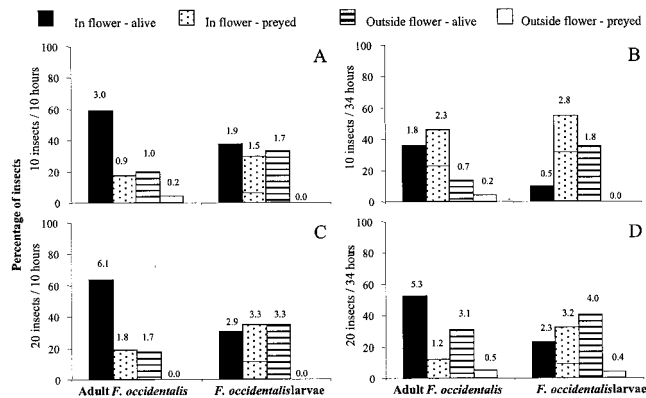


Fig. 2. Distribution and status of second instar and adult female *F. occidentalis*, at different densities and times after release onto a pepper flower, in the presence of *O. insidiosus*. The different densities and time intervals are (A) 10 insects at 10-h postrelease, (B) 10 insects at 34-h postrelease, (C) 20 insects at 10-h postrelease, and (D) 20 insects at 34-h postrelease. Numbers above bars are means.

three outer flowers. The mean number of *F. tritici* per flower was  $2.6 \pm 1.00$  in the central flower compared with  $0.6 \pm 0.33$  in the three other flowers. In the 34-h exposure, the mean number of *F. occidentalis* per flower dropped to  $2.3 \pm 0.83$  in the central flower compared with  $0.6 \pm 0.29$  in the three outer flowers. The mean number of *F. tritici* per flower was  $1.2 \pm 0.66$  in the central flower compared with  $0.9 \pm 0.17$  in the three other flowers.

In the two high-density treatments, there was a significant species  $\times$  location interaction, indicating that the distribution was dependent upon species (Table 3; Fig. 3). *F. tritici* females were more likely than *F. occidentalis* females to disperse from the central release flower in the 10-h exposure (contrast for interaction between species and location either inside or outside of flowers:  $\chi^2 = 5.62$ ,  $df = 1$ ,  $P = 0.018$ ). In the 34-h exposure, most of the thrips had dispersed from the central release flower (Fig. 3), with a greater proportion of *F. tritici* than *F. occidentalis* having moved outside of any flower (contrast for interaction between species and location either inside flowers or outside of flowers:  $\chi^2 = 15.45$ ,  $df = 1$ ,  $P < 0.0001$ ). The distribution of thrips was the most uniform in this time and density combination. The mean number of *F. occidentalis* per flower was  $2.7 \pm 1.07$  in the central flower compared with  $2.1 \pm 0.36$  in the three outer flowers. The mean number of *F. tritici* per flower was  $1.6 \pm 1.08$  in the central flower compared with  $1.73 \pm 0.37$  (per flower) in the three outer flowers.

**Dispersal of *F. occidentalis* and *F. tritici* in the Presence of *O. insidiosus*.** In the 10-h exposure trials, there was no significant difference in predation by *O. insidiosus* between the thrips species (Table 4; Fig. 4). Predation occurred in all of the flowers as well as outside of the flowers, but the mean number of prey taken was only  $0.3 \pm 0.34$  for *F. occidentalis* (34% of prey captured) and  $0.6 \pm 0.90$  for *F. tritici* (66% of prey) in the 10-h low-density exposure. In the high-density 10-h exposure trials, 57% of the prey captured were *F. tritici* ( $1.3 \pm 1.00$ ) and 43% were *F. occidentalis* ( $1.0 \pm 0.58$ ). The distribution of species did vary in both of the 10-h exposure treatments (Table 4). A significantly greater proportion of *F. tritici* than *F. occidentalis* was located outside of the flowers in the low-density 10-h exposure and in the high-density 10-h exposure (contrasts for interaction between species and location either inside flowers or outside of flowers:  $\chi^2 = 10.46$ ,  $df = 1$ ,  $P = 0.0012$ , and  $\chi^2 = 5.70$ ,  $df = 1$ ,  $P = 0.017$ , respectively).

In the low-density 34-h exposure, most of the thrips dispersed from the central release flower to the other flowers (Fig. 4), but most of the predation occurred in the central flower. The risk of predation was significantly greater for thrips in the central flower than in the outer flowers (contrast for interaction between status and location either inside central flower or outer flowers:  $\chi^2 = 4.38$ ,  $df = 1$ ,  $P = 0.036$ ). The majority of the prey captured were *F. tritici* (80%) (Table 4). Of the total prey killed, 50% were in the central flower,

Table 3. Maximum likelihood ANOVA for model parameters of prey type, and location for different densities and time exposures of *F. occidentalis* and *F. tritici* in the absence of *O. insidiosus*

Effect <sup>a</sup>	df	10 Insects/10 h		10 Insects/34 h		20 Insects/10 h		20 Insects/34 h	
		$\chi^2$	P	$\chi^2$	P	$\chi^2$	P	$\chi^2$	P
Location	2	37.93	<0.0001	7.78	0.0204	13.38	0.0012	51.94	<0.0001
Species	1	0.04	0.8415	0.00	1.0000	0.19	0.6666	0.70	0.4016
Location $\times$ species	2	-	-	-	-	9.20	0.0100	14.18	0.0008

<sup>a</sup> Location = in central flower, or in other flowers, or outside flowers. Species = *F. occidentalis* or *F. tritici*. Effects without corresponding statistical entries in table were not included in the final model for the respective density and time treatment.



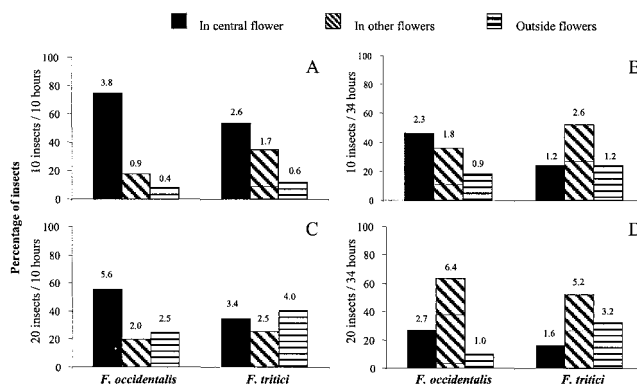


Fig. 3. Distribution of adult female *F. occidentalis* and *F. tritici*, at different densities and times after release onto a central pepper flower, in the absence of *O. insidiosus*. The different densities and time intervals are (A) 10 insects at 10-h postrelease, (B) 10 insects at 34-h postrelease, (C) 20 insects at 10-h postrelease, and (D) 20 insects at 34-h postrelease. Numbers above bars are means.

30% were in the other flowers, and 20% were outside of the flowers.

In the high-density 34-h exposure, the distributions of *F. occidentalis* and *F. tritici* differed significantly (Table 4; Fig. 4). The majority of both *F. occidentalis* and *F. tritici* had dispersed from the release flower. A significantly greater proportion of the thrips outside of flowers was *F. tritici* (contrast for interaction between species and location either inside flowers or outside of flowers:  $\chi^2 = 28.33$ ,  $df = 1$ ,  $P < 0.0001$ ). The risk of predation did not differ between *F. occidentalis* and *F. tritici*. The mean number of *F. occidentalis* preyed upon was  $2.7 \pm 1.61$ , and the mean number of *F. tritici* preyed upon was  $2.1 \pm 1.44$ . However, the risk of predation was significantly lower for thrips in the outer flowers than for thrips in the central release flower (contrast for interaction between status and location either inside central flower or outer flowers:  $\chi^2 = 5.03$ ,  $df = 1$ ,  $P = 0.025$ ). This time and density combination had the highest proportion of thrips outside of the flowers and the greatest proportion of predation occurring outside of the flowers.

## Discussion

In the current study, we examined the distribution of different life stages of *F. occidentalis*, and of females of *F. occidentalis* and *F. tritici* among pepper flowers in

the absence and presence of the predator *O. insidiosus*. Both *Frankliniella* spp. and *O. insidiosus* aggregate in pepper flowers (Hansen et al. 2003), as well as the flowers of other host plants (e.g., Pickett et al. 1988, Rosenheim et al. 1990, Atakan et al. 1996, Clements and Yeargan 1997). Differences in the behavior of larval and adult *F. occidentalis*, and in the behavior of adult *F. occidentalis* and *F. tritici* females affected their distributions, which consequently affected interactions with the predator *O. insidiosus*. *O. insidiosus* preferentially fed on larvae compared with adults. There was no discernable preference of *O. insidiosus* between the adults of *F. occidentalis* and *F. tritici*. Most predation occurred in the flowers. The predator actively searched among the flowers for prey.

The predation levels were lower than those reported in some other studies (Sabelis and Van Rijn 1997 and references therein; Venzon et al. 2000). However, those studies used structurally simple environments, such as filter paper or leaf discs in confined arenas. In our experiments, we used flowers to simulate the structurally complex environments where interactions between these thrips and *O. insidiosus* occur in the field. *F. occidentalis* and *F. tritici*, as well as *O. insidiosus*, are strongly concentrated in the flowers of pepper (Hansen et al. 2003). Venzon et al. (2000) showed that predation by *O. laevigatus* (Fieber) on *F. occidentalis* larvae was lower in more

Table 4. Maximum likelihood ANOVA for model parameters of predation, location, and species type for different densities and time exposures of *F. occidentalis* and *F. tritici* to *O. insidiosus*

Effect <sup>a</sup>	df	10 Insects/10 h		10 Insects/34 h		20 Insects/10 h		20 Insects/34 h	
		$\chi^2$	P	$\chi^2$	P	$\chi^2$	P	$\chi^2$	P
Predation	1	45.21	<0.0001	29.97	<0.0001	84.76	<0.0001	33.10	<0.0001
Location	2	13.74	0.0010	2.70	0.2591	33.74	<0.0001	19.92	<0.0001
Species	1	0.48	0.4870	3.20	0.0737	1.70	0.1928	1.40	0.2361
Location $\times$ species	2	9.19	0.0101	5.84	0.0539	5.58	0.0614	28.17	<0.0001
Predation $\times$ species	1	-	-	4.92	0.0265	-	-	-	-
Predation $\times$ location	2	-	-	6.44	0.0400	-	-	8.57	<0.0001

<sup>a</sup> Predation = alive or dead. Location = in or out of the flower. Species = *F. occidentalis* or *F. tritici*. Effects without corresponding statistical entries in table were not included in the final model for the respective density and time treatment.

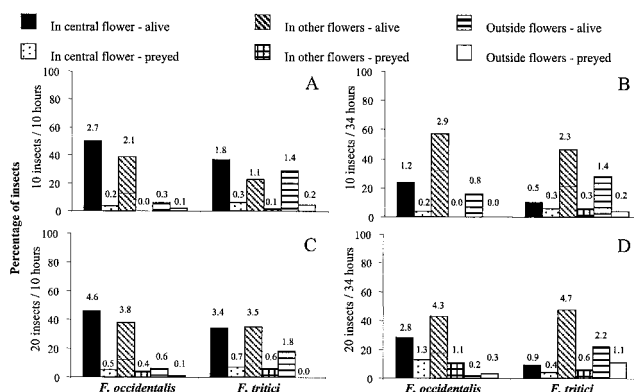


Fig. 4. Distribution and status of adult female *F. occidentalis* and *F. tritici*, at different densities and times after release onto a central pepper flower, in the presence of *O. insidiosus*. The different densities and time intervals are (A) 10 insects at 10-h postrelease, (B) 10 insects at 34-h postrelease, (C) 20 insects at 10-h postrelease, and (D) 20 insects at 34-h postrelease. Numbers above bars are means.

complex environments. Predation also was lower in larger arenas, where thrips may escape from a predator (Isenhour and Yeargan 1981). The density of thrips affected predation rates (Sabelis and Van Rijn 1997). At low prey densities, predators may spend substantial amounts of time searching for more profitable sites, which would further reduce predation rates. *O. insidiosus* also feeds on pollen (Kiman and Yeargan 1985). Having this alternative food source may have reduced predation on thrips.

**Adult and Second Instars of *F. occidentalis*.** When *O. insidiosus* was absent, significantly more second instars than adults of *F. occidentalis* moved out of the flower, and the proportion of larvae moving out of the flower increased dramatically with time. This movement by larvae in the absence of predators may be a function of their developmental stage. Second instars stop feeding and leave the flower to pupate (Robb and Parella 1991, Sabelis and Van Rijn 1997). Under similar experimental conditions, the duration of the second instar for *F. occidentalis* is  $\approx 3$ –4 d (Deangelis et al. 1993, Reitz et al. 2002). Therefore, by the end of the 34-h exposure period, the larvae would have been nearing pupation, and thus increasing the likelihood to leave the flower. Thrips larvae and adults also may have moved in search of new food resources (Kirk 1997), in which case adults would be better able to return to the available flower in the experimental arena than larvae.

We observed similar dispersal from the flowers of pepper when the predator *O. insidiosus* was present. Although the number of thrips was reduced by predation, >50% of the live larvae were located outside of the flower. In addition to the developmental and foraging factors, this movement also may have been in response to predation. Second instars of *F. occidentalis* release an alarm pheromone when attacked by *O. insidiosus*, which can induce conspecific larvae to disperse (Teerling et al. 1993). *F. occidentalis* will move away from predators that have recently fed on thrips (Venzon et al. 2000). The proportions of adults outside of the flower increased when *O. insidiosus* was

present, which further suggests that dispersal was in response to the presence of the predator.

Although larvae were more likely than adults to disperse from the flower, *O. insidiosus* preyed upon more larvae. A key factor in prey selection is the vulnerability of prey (Lang and Gsödl 2001). Because thrips larvae move slower than adults, larvae should be more vulnerable to predation (Sabelis and Van Rijn 1997, van den Meiracker and Sabelis 1999). Isenhour and Yeargan (1981) showed in no-choice tests that *O. insidiosus* killed more larvae than adults of soybean thrips, *Neohydatothrips variabilis* (Beach). Likewise, predation by *O. minutus* (L.) is greater against *F. occidentalis* larvae than adults (Lichtenauer and Sell 1993).

At the low density of 10 thrips per arena, predation reduced the number of larvae available over time. This lower availability of larvae probably forced *O. insidiosus* to prey more on the adults. The absolute amount of predation by *O. insidiosus* was twice as much in high-density treatments as in the low-density treatments. However, as time increased at a high density of prey, numbers of larvae and adults killed by *O. insidiosus* remained similar, suggesting that *O. insidiosus* became satiated.

***F. occidentalis* and *F. tritici*.** When *O. insidiosus* were absent, *F. tritici* dispersed from the flower more than *F. occidentalis*. *F. occidentalis* were more likely to be in the flowers, especially the central release flower. *F. tritici* were more active, and they dispersed from the central flower more than *F. occidentalis*. These results corroborate the findings of Hansen et al. (2003), showing that *F. tritici* is more active than *F. occidentalis*, and of Ramachandran et al. (2001), who suggested that *F. tritici* is more active than *F. occidentalis*. The changing densities among flowers over time indicate that adults of both species will move, possibly to locate additional feeding or oviposition sites.

The presence of *O. insidiosus* caused a behavioral change in both thrips species. When *O. insidiosus* was present, *F. tritici* and *F. occidentalis* were more likely to disperse from the central flower to the other loca-

tions. *F. occidentalis* were more active when *O. insidiosus* was present than when it was not present. The increased activity suggests that the adults of *F. occidentalis* and *F. tritici* were able to detect the presence of *O. insidiosus* and disperse in attempts to avoid predation. *O. insidiosus* may have been attracted first to the central release flower because of the high densities of thrips initially located there. However, predation occurred in all of the flowers and outside of the flowers, indicating that *O. insidiosus* also moved readily among flowers.

The movement of *O. insidiosus* and *F. tritici* in the arena actually may have increased the chances of encounters compared with encounters between *O. insidiosus* and the more sedentary *F. occidentalis*. If so, we may expect overall predation to be greater against *F. tritici*. However, this was the case in only the 34 h/10 thrips/time and density combination. Encounter rate is a determinant of risk of predation, but greater success in attacks may counterbalance differences in encounters, leading to similar preferences for different prey (Allan et al. 1987, Reitz et al. 2002).

Many factors are involved in how *O. insidiosus* chooses prey, and these factors include the type, density, vulnerability, and mobility of a prey. In the current study, *O. insidiosus* successfully preyed on all types of prey that were offered, although it dealt differently with each type of prey. From a population dynamics perspective, the ability of *O. insidiosus* to capture different species and developmental stages of thrips is an important factor in its ability to regulate thrips populations (Funderburk et al. 2000, Ramachandran et al. 2001).

### Acknowledgments

We appreciate the assistance of Julianne Stavisky, University of Florida, and Eric Hansen, United States Department of Agriculture-Agricultural Research Service, in conducting this project. This research was supported, in part, by specific cooperative agreement 58-6615-8-022 between United States Department of Agriculture-Agricultural Research Service and Florida A&M University.

### References Cited

- Allan, J. D., A. S. Flecker, and N. L. McClintock. 1987. Prey preference of stoneflies: sedentary vs mobile prey. *Oikos* 49: 323–331.
- Atakan, E., M. Coll, and D. Rosen. 1996. Within-plant distribution of thrips and their predators: effects of cotton variety and developmental stage. *Bull. Entomol. Res.* 86: 641–646.
- Chellemi, D. O., J. E. Funderburk, and D. W. Hall. 1994. Seasonal abundance of flower-inhabiting *Frankliniella* species (Thysanoptera: Thripidae) on wild plant species. *Environ. Entomol.* 23: 337–342.
- Clements, D. J., and K. V. Yeorgan. 1997. Seasonal and intraplant distribution of *Orius insidiosus* (Hemiptera: Anthocoridae) on soybean and possible interactions with *Nabis roseipennis* (Hemiptera: Nabidae). *J. Kansas Entomol. Soc.* 70: 94–99.
- Cloutier, C., and S. G. Johnson. 1993. Predation by *Orius triticolor* (Hemiptera: Anthocoridae) on *Phytoseiulus persimilis* (Acarina: Phytoseiidae) testing for compatibility between biocontrol agents. *Environ. Entomol.* 22: 477–482.
- Coll, M., and J. R. Ruberson. 1998. Predatory Heteroptera: an important yet neglected group of natural enemies, pp. 1–6. In M. Coll and J. R. Ruberson (eds.), *Thomas Say Publications in Entomology Proceedings: predatory Heteroptera: their ecology and use in biological control*. Entomological Society of America, Lanham, MD.
- Deangelis, J. D., D. M. Sether, and P. A. Rossignol. 1993. Survival, development, and reproduction in western flower thrips (Thysanoptera: Thripidae) exposed to impatiens necrotic spot virus. *Environ. Entomol.* 22: 1308–1312.
- Fritsche, M. E., and M. Tamo. 2000. Influence of thrips prey species on the life-history and behaviour of *Orius albidipennis*. *Entomol. Exp. Appl.* 96: 111–118.
- Funderburk, J., J. Stavisky, and S. Olson. 2000. Predation of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in field peppers by *Orius insidiosus* (Hemiptera: Anthocoridae). *Environ. Entomol.* 29: 376–382.
- Hansen, E. A., J. E. Funderburk, S. R. Reitz, J. Eger, S. Ramachandran, and H. J. McAuslane. 2003. Within plant distribution of *Frankliniella* thrips and *Orius insidiosus* on field pepper. *Environ. Entomol.* (in press).
- Isenhour, D. J., and K. V. Yeorgan. 1981. Predation by *Orius insidiosus* on the soybean thrips, *Sericothrips variabilis*: effect of prey stage and density. *Environ. Entomol.* 10: 496–500.
- Kiman, Z. B., and K. V. Yeorgan. 1985. Development and reproduction of the predator *Orius insidiosus* (Hemiptera, Heteroptera: Anthocoridae) reared on diets of selected plant material and arthropod prey. *Ann. Entomol. Soc. Am.* 78: 464–467.
- Kirk, W. D. J. 1997. Distribution, abundance and population dynamics, pp. 217–257. In T. Lewis (ed.), *Thrips as crop pests*. CAB International, New York.
- Lang, A., and S. Gsödl. 2001. Prey vulnerability and active predator choice as determinants of prey selection: a carabid beetle and its aphid prey. *J. Appl. Entomol.* 125: 53–61.
- Lichtenauer, A., and P. Sell. 1993. Predation of different developmental stages of the western flower thrips by adults of *Orius minutus* (Heteroptera: Anthocoridae). *Med. Fac. Landbouww. Univ. Gent* 58: 397–407.
- Pickett, C. H., L. T. Wilson, and D. Gonzalez. 1988. Population dynamics and within-plant distribution of the western flower thrips (Thysanoptera: Thripidae), an early-season predator of spider mites infesting cotton. *Environ. Entomol.* 17: 551–559.
- Ramachandran, S., J. Funderburk, J. Stavisky, and S. Olson. 2001. Population abundance and movement of *Frankliniella* species and *Orius insidiosus* in field pepper. *Agric. Forest Entomol.* 3: 1–10.
- Reitz, S. R., J. E. Funderburk, E. A. Hansen, I. Baez, S. Waring, and S. Ramachandran. 2002. Interspecific variation in behavior and its role in thrips ecology, pp. 133–140. In R. Marullo and L. A. Mound (eds.), *Thrips and tospoviruses: Proceedings of the 7th International Symposium on Thysanoptera*, July 2–7, Reggio Calabria, Italy. Australian National Insect Collection, Canberra.
- Robb, K. L., and M. P. Parella. 1991. Western flower thrips, a serious pest of floricultural crops, pp. 343–357. In B. L. Parker, M. Skinner, and T. Lewis (eds.), *Proceedings of the International Conference on Thrips*, Feb. 21–23, 1989, Burlington, VT U.S.A. United States Department of Agriculture Forest Service, Northeastern Forest Experiment Station, Radnor, PA.



- Rosenheim, J. A., S. C. Welter, M. W. Johnson, R.F.L. Mau, and L. R. Gusukuma-Minuto. 1990. Direct feeding damage on cucumber by mixed-species infestations of *Thrips palmi* and *Frankliniella occidentalis* (Thysanoptera: Thripidae). *J. Econ. Entomol.* 83: 1519–1525.
- Sabelis, M. W., and P. C. J. Van Rijn. 1997. Predation by mites and insects, pp. 259–354. *In* T. Lewis (ed.), *Thrips as crop pests*. CAB International, Wallingford, UK.
- Saint-Cyr, J. F., and C. Cloutier. 1996. Prey preference by the stinkbug *Perillus bioculatus*, a predator of the Colorado potato beetle. *Biol. Contr.* 7: 251–258.
- Salas-Aguilar, J., and L. E. Ehler. 1977. Feeding habits of *Orius tristicolor*. *Ann. Entomol. Soc. Am.* 70: 60–62.
- SAS Institute. 1989. SAS/STAT user's guide, vol. 1. SAS Institute, Cary, NC.
- Schoenig, S. E., and L. T. Wilson. 1992. Patterns of spatial association between spider mites (Acari: Tetranychidae) and their natural enemies on cotton. *Environ. Entomol.* 21: 471–477.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. Freeman, New York.
- Teerling, C. R., H. D. Pierce, J. H. Borden, and D. R. Gillespie. 1993. Identification and bioactivity of alarm pheromone in the western flower thrips, *Frankliniella occidentalis*. *J. Chem. Ecol.* 19: 681–697.
- Toapanta, M., J. Funderburk, S. Webb, D. Chellemi, and J. Tsai. 1996. Abundance of *Frankliniella* spp. (Thysanoptera: Thripidae) on winter and spring host plants. *Environ. Entomol.* 25: 793–800.
- van den Meiracker, R.A.F., and P.M.J. Ramakers. 1991. Biological control of the western flower thrips *Frankliniella occidentalis* in sweet pepper with the anthocorid predator *Orius insidiosus*. *Mededelingen van de Faculteit Landbouwwetenschappen Universiteit Gent* 56: 241–249.
- van den Meiracker, R.A.F., and M. W. Sabelis. 1999. Do functional responses of predatory arthropods reach a plateau? A case study of *Orius insidiosus* with western flower thrips as prey. *Entomol. Exp. Appl.* 90: 323–329.
- Venzon, M., A. Janssen, A. Pallini, and M. W. Sabelis. 2000. Diet of a polyphagous arthropod predator affects refuge seeking of its thrips prey. *Anim. Behav.* 60: 369–375.

*Received 15 September 2003; accepted 2 February 2004.*